A new theory that fills the missing link between sizes of unicellular organisms and their resource molecules (Theory of Biomathematics and its Applications IV)

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A new theory that fills the missing link between sizes of unicellular organisms and their resource molecules [1]

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1 Introduction

Resource uptake by microorganisms, such as bacteria and phytoplankton, is inevitably limited by diffusive transport of resource molecules [10, 6, 7]. In this study, I introduce a new model of consumer-resource dynamics in aquatic environments that considers mechanistic details of resource uptake process. Here I formulate resource uptake as a three-step process: (i) transport of resource molecules from the medium to the cell surface via molecular diffusion, (ii) resource uptake by membrane transporters, and (iii) enzymatic catalysis within a cell.

Because molecular diffusion coefficients are inversely proportional to sizes of resource molecules according to the Stokes-Einstein equation, resource sizes affect consumer-resource dynamics by changing the efficiency of diffusive transport. This model is the first to link sizes of microorganisms with sizes of their resource molecules, providing new insight to the resource competition theory.

2 Mechanistic model of resource uptake

We consider spherical cells that take up resource molecules dissolved in a fluid. First, resource molecules are transported by molecular diffusion from medium to cell surface. Once resource molecules reach the cell surface, they are taken up actively by membrane transporter proteins, kept temporally in the internal storage pool, and then utilized for cell growth. Thus resource molecules are taken up by a cell via these three steps: diffusive transport, membrane uptake, and cellular catalysis.

The first step, diffusive transport solely relies on molecular diffusion at the scale of unicellular organisms [7]. In polar coordinate system, this step can be described by:

$$\frac{\partial R}{\partial t} = \frac{D}{r^2}\frac{\partial}{\partial r}\left(r^2\frac{\partial R}{\partial r}\right), \tag{1}$$

where t is time; r is the distance from the center of a cell; R is the resource concentration; and D is the molecular diffusion coefficient. The boundary conditions are: $R(r_0) = R_0$ at cell surface ($r = r_0$), and $R(r_{\mathrm{BL}}) = \bar{R}$ at the edge of the diffusive boundary layer [4], where $\bar{R}$ is the resource concentration in the medium. While $\bar{R}$ is what we usually consider as "resource concentration" both theoretically and empirically, R_0 is what a cell actually experiences in the resource uptake process.

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The second step, the membrane uptake, is described by a function of resource concentration at cell surface, R_0, and amount of internal storage of resource, Q [11, 3]:

$$4\pi r_0^2 f(R_0, Q), \tag{2}$$

where $f(R_0, Q)$ is the uptake rate per unit cell surface area. In most studies, f is an increasing function of R_0 with negative feedback from Q: $\partial f/\partial R_0 \geq 0$ and $\partial f/\partial Q \leq 0$ [11, 3].

The last step, enzymatic catalysis, is described by a function of internal storage, Q,

$$\frac{4}{3}\pi r_0^3 g(Q), \tag{3}$$

where $g(Q)$ is the rate per unit cell volume. The catalysis rate increases with internal storage, $\partial g/\partial Q \geq 0$.

Equations (1)–(3) describe the three steps of mechanistic resource uptake. Most studies consider step 2 only, or step 2 and 3, which correspond to the well-known Droop model [2, 3].

3 Example: chemostat model

The mechanistic resource uptake model can be applied to consumer-resource dynamics. Here I consider a chemostat model. The dynamics of resource concentration in medium ($\bar{R}$), internal storage (Q), and cell density (B) is expressed by

$$\frac{d\bar{R}}{dt} = \kappa(R_{\mathrm{IN}} - \bar{R}) - J_{\mathrm{BL}}B \tag{4a}$$

$$\frac{dQ}{dt} = 4\pi r_0^2 f(R_0, Q) - \frac{4}{3}\pi r_0^3 g(Q) \tag{4b}$$

$$\frac{dB}{dt} = B\left(\frac{4/3\pi r_0^3 g(Q)}{Q} - \theta r_0^{\rho} - \kappa\right), \tag{4c}$$

where κ is dilution rate of chemostat and θr_0^{ρ} is size dependent loss rate such as respiration, sinking, or grazing mortality. J_{BL} is the resource flux at the edge of the diffusive boundary layer:

$$J_{\mathrm{BL}} = 4\pi r_{\mathrm{BL}}^2 D \frac{\partial R}{\partial r}\bigg|_{r=r_{\mathrm{BL}}}. \tag{5}$$

The change in R_0 is the difference between membrane uptake and diffusive flux at $r = r_0$:

$$\frac{dR_0}{dt} = -f(R_0, Q) + D\frac{\partial R}{\partial r}\bigg|_{r=r_0}. \tag{6}$$

Diffusive transport at micro meter scale and enzymatic process within cells are generally much faster than resource and biomass dynamics [10]. In this case, resource flux through the three steps is constant, that is, equations (1), (6), and (4b) are at their steady state. Taking the right hand side of (1) to be 0, resource flux J through diffusive transport is obtained:

$$J = 4\pi r_0 D(\bar{R} - R_0)\frac{r_{\mathrm{BL}}}{r_{\mathrm{BL}} - r_0}, \tag{7}$$

which equates with other two steps. Taking right hands sides of (6) and (4b), we have the steady state resource flux:

$$J = 4\pi r_0 D(\bar{R} - R_0)\frac{r_{BL}}{r_{BL} - r_0} = 4\pi r_0^2 f(R_0, Q) = \frac{4}{3}\pi r_0^3 g(Q). \tag{8}$$

Then the reduced chemostat system is written by

$$\frac{d\bar{R}}{dt} = \kappa(R_{IN} - \bar{R}) - JB \tag{9a}$$

$$\frac{dB}{dt} = B\left(\frac{J}{Q} - \theta r_0^{\rho} - \kappa\right). \tag{9b}$$

The above reduced system was analyzed in [14]. The theory revealed a counterintuitive relationship between sizes of resource molecules and the optimal cell size (i.e., size of a competitor that outcompetes others); the optimal cell size negatively depends on resource molecule size.

This model can be easily extended to multi-species competition. In [14], two different-sized competitors are shown to coexist on two resources of different sizes.

4 Concluding remarks

Ecologists generally expect a positive relationship between sizes of prey and predator in food webs [1, 13]. Then, can we also expect the same positive relationship between sizes of microorganisms and their resource molecules? The new theory gave the answer to the question. Changes in resource molecule sizes do change sizes of the consumers, but to the opposite direction of what we generally expect; larger resource molecules favor smaller consumers. Though experiments explicitly designed to test this prediction have not been done yet, it is already supported by several experiments [8, 9].

In previous theories, trade-offs in the uptake of resources are necessary to achieve coexistence [12]. In [14], in contrast, no explicit trade-offs are incorporated in the model; both resources and consumers are identical except their sizes. Rather than presuming explicit trade-offs, they are derived from the biophysical principle of resource uptake.

There are infinite variation in sizes of resource molecules, such as various-sized sugars, amino acids, proteins, and polysaccharides. The theory suggests that variation in size of resource molecules alone, regardless of the quality, can promote diversity of microorganisms, giving a new dimension of ecological niche space— the size of resource molecules. Because size variation of resource molecules is unlimited, this partly resolves "the paradox of plankton," which questioned the huge diversity of planktonic organisms on limited number of resources [5].

The analysis of the full model (4a)–(4c) is yet to be done. Further studies on this model may consider continuous size ranges of both cell and resource molecules, resource fluctuations, or individual based approach. As the simple Michaelis-Menten kinetics was replaced by the Droop equation to account for the variable internal storage of cells during resource uptake [2, 11, 3], this new model adds another new step to the theory of consumer-resource dynamics.

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